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Bioenergetic consequences of warming rivers to adult Atlantic salmon *Salmo salar* during their spawning migration

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Abstract

1. Climate change poses a challenge to wild fishes, yet little is known about the behavioural use and metabolic consequences of thermally heterogeneous water encountered by wild salmon during their energetically demanding upstream spawning migration.
2. Temperature, body size and activity levels were modelled to predict energy depletion of salmon during their spawning migration in rivers. Archival temperature loggers revealed the thermal habitat of adult migrating Atlantic salmon (*Salmo salar* Salmonidae), which we used to apply bioenergetics models that estimated size-dependent temperature-driven metabolic expenditures as part of the costs of the migration.
3. Between July 16 and August 19, the mean water temperature experienced by salmon (t_{FISH}) ranged from 11.5 to 18.0°C (14.5 ± 1.2 *SD* °C) and closely followed the ambient surface water temperature (t_{RIVER}) of the river (11.5–18.5°C; 14.8 ± 1.4°C) such that the regression equation $t_{\text{FISH}} = 3.24 + 0.76$ (t_{RIVER}) was highly correlated with observations ($R^2 = 0.94$).
4. Although temperature increases were predicted and confirmed to increase energetic costs, rates of energy depletion were more sensitive to changes in swimming speed and body size than to temperature increases in the range explored for this system.
5. We conclude that warming could contribute to changing life history phenotypes of salmon in some rivers, for example, delayed river entry or reduced probability of iteroparity, with potentially more dire consequences for smaller individuals.

KEYWORDS
bioenergetics, fisheries, iButton, iteroparity, telemetry

1 | INTRODUCTION

Temperature constrains the distribution of species (Pörtner, 2002) and influences the timing and expression of many life history events (Walther, Post, Convey, & Menzel, 2002) such as breeding, aestivation/hibernation and migration (Lennox, Chapman, et al., 2016). For ectotherms such as most fishes, temperature directly controls, and can ultimately limit, the rates of enzymatic, metabolic and cardiac processes (Behrisch, 1969; Farrell, Eliason, Sandblom, & Clark, 2009; Fry, 1971). At temperatures beyond optimum, the tissue demands for oxygen increase (Pörtner & Knust, 2007) but the capacity to deliver that oxygen decreases (i.e. decline in aerobic scope; Priede,

1977) until glycolytic ATP production replaces aerobic respiration (i.e. anaerobiosis; Pörtner, 2002). Warm water temperature can be energetically taxing (Katinic, Patterson, & Ydenberg, 2015; Rand et al., 2006), accelerate maturation (Morbey, Brassil, & Hendry, 2005) and promote pathogen infection and development (Harvell et al., 2002).

In many rivers, water temperature is increasing due to climate change (Caissie, 2006; Mote et al., 2003; Webb, 1996). This is a particular concern in the Arctic where water temperatures are projected to increase at a faster pace than at lower latitudes (O'Brien, Sygna, & Haugen, 2004; Prowse et al., 2006). As water temperatures rise, the costs of freshwater residence will be altered and ectotherm biology will be affected (Crozier et al., 2008; Jonsson & Jonsson, 2009). There are many freshwater animals in coastal zones that use both marine and freshwater environments to complete their life history. Migrants must negotiate the two environments and allocate energy such that their rate of energy depletion does not exceed physiological limits or energetic reserves (Burnett et al., 2014; Hodgson & Quinn, 2002). As temperatures increase, the physiology and behaviour of freshwater animals are expected to reflect higher energetic costs of residence and activity (Crozier & Hutchings, 2014). Energetic models provide tools for ecologists to investigate energy allocation of animals; energy acquisition must be balanced against depletion, which depends on the individual's size, activity and the water temperature (Brett, 1971; Fry, 1971; Kingsolver & Huey, 2008). Individuals must allocate energy during the migration efficiently with a goal of successfully participating in spawning and other life history events, which yields considerable diversity in physiological and behavioural phenotypes to promote survival (Glebe & Leggett, 1981; Jonsson, Jonsson, & Hansen, 1997; Standen, Hinch, Healey, & Farrell, 2002).

Atlantic salmon (*Salmo salar* Salmonidae) have a Holarctic distribution and rely on fresh water for spawning and nursery grounds. Adults return from the sea to spawn at various sizes, often with an earlier timed river entry associated with southern latitudes that have warmer temperature regimes (Heggberget, 1988; Klemetsen et al., 2003; Thorstad, Whoriskey, Rikardsen, & Aarestrup, 2011). Freshwater residence is also briefer for many adult salmon at the northern edge of their range, although some individuals enter more than a year before reproducing. Timing of entry is known to depend upon river characteristics as well as individual size (Jonsson, Hansen, & Jonsson, 1991), and salmon can exhibit a refuging behaviour during the migration as a maintenance strategy (Frechette, Dugdale, Dodson, & Bergeron, 2018; Richard, Bernatchez, Valiquette, & Dionne, 2014). When salmon enter fresh water they cease feeding, such that stored energy must then suffice for migration, completion of sexual maturation and spawning (Moore, 1997). Iteroparous migrants such as Atlantic salmon must also preserve enough energy after spawning for its return to the ocean where it can begin the reconditioning process for subsequent migration and reproduction (Halttunen et al., 2013; Jonsson, Jonsson, & Hansen, 1991; Jonsson et al., 1997). The Arctic is an area of relatively sparse human habitation and impact; therefore, climate change may present one of the most salient threats to salmon in the north. The phenotypic plasticity of salmon means that they may adjust either their body size through changes to maturation schedules or their behaviour by shifting run timing to adapt to changing demands associated with climate change (Clark et al., 2012; Dempson et al., 2017; Otero et al., 2014). Models predicting the energetic costs of size, activity and water temperature will therefore yield a better understanding of Atlantic salmon migration and potential responses to climate change.

Animal size, activity and temperature contribute simultaneously to the metabolic rate and the energy demands upon the individual. Warming temperatures portend bioenergetic failure of some organisms (Farrell et al., 2008; Rummer et al., 2014) and the temperature-size rule posits that smaller organisms should be favoured at warmer temperature regimes (Kingsolver & Huey, 2008). Given that thermal ecology of adult Atlantic salmon during their freshwater migration is poorly understood (Bardonnet & Baglinière, 2000), we designed a study to investigate the contributions of water temperature and size, along with swimming activity, to energetic depletion of this anadromous fish on its spawning migration in fresh water. We hypothesised that all three variables (size, swimming activity and temperature) would influence energy demands on individuals, which would imply that climatic changes will accelerate the rate of energy depletion of freshwater fish during their migration.

2 | METHODS

2.1 | Study area

We studied a population of Atlantic salmon in the Lakselva River in Finnmark, Norway. These Atlantic salmon enter the river from May to September (E. Liberg, personal communication), but based on quantitative catch records, the majority begin their freshwater migration in July and August (www.scanatura.no). The Lakselva River flows through two lakes, Øvrevatnet and Nedrevatnet (Figure 1). River discharge is measured at Skoganvarre (69°50′13.2″N 25°05′07.5″E), encompassing 61% of the watershed, which can be extrapolated to estimate total discharge (T. Havn, unpublished). Estimated average yearly discharge from 2000 to 2016 was 24 ± 2.2 m^3/s (range = 21–33 m^3/s). The river also has one major tributary, which flows into Lake Nedrevatnet. Most salmon hold within the river just below the lakes (Lennox, Cooke, et al., 2016) until spawning begins in October (E. Liberg, personal communication). After spawning, surviving Atlantic salmon typically overwinter in the river as kelts and then exit the following spring to recondition at sea.

Lakselva has a catchment area of 1,536 km^2 and the mainstem of the river has 45 km available to salmon for spawning habitat. Lakselva River drains into the Porsangerfjord within the administrative district of the municipality of Lakselv (70°03′55.2″N 24°55′43.8″E). To monitor ambient river water temperature, we deployed four HOBO temperature loggers (HOBO Pendant Temperature/Light Data Logger 64K-UA-002-64, Onset, MA) in the river from July 17 to October 24, 2014 (see Supporting Information for description of logger calibration). One river temperature data logger was stationed in

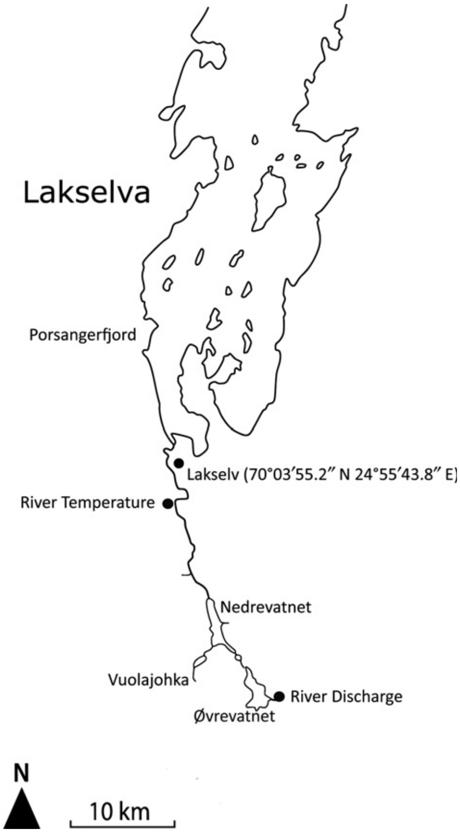

FIGURE 1 Lakselva in Porsanger, Finnmark, Norway. The watershed incorporates two major lakes, Øvrevatnet and Nedrevatnet. Atlantic salmon return to Lakselva from the ocean via the Porsangerfjord throughout the summer and migrate upriver to spawning grounds. The location of the river temperature logger and river discharge metre is indicated on the map. For this study, all tagged salmon remained in Lakselva below the lakes throughout their migration. Note that the river flows from south to north, draining into the Porsangerfjord

the lower section of the river, one in Lake Nedrevatnet and one in the upper section of the river; all were placed approximately one metre below the surface (Figure 1). The river monitoring stations recorded water temperature every 10 min. Previous monitoring by the Lakselva Landowners Association observed little variability of the surface water temperatures among sites in the lower reach of the river (E. Liberg, personal communication).

2.2 | Sampling

We cooperated with local anglers and captured Atlantic salmon for our experiment from July 7 to August 29, 2014. Cooperation with local anglers encouraged engagement of locals and other stakeholders in the work and was important for ensuring that logging tags from recaptured salmon were returned. Only experienced salmon anglers participated and we did not tag any salmon that was in poor condition because of angling (i.e. critical hooking, extreme bleeding; Lennox, Cooke, et al., 2016). Twenty-one Atlantic salmon (mean = 90 ± 16 cm *SD* TL, range: 62–121 cm) were double-tagged with radio-transmitting tags in the frequency range 142.114–142.213 (model F2120; Advanced Telemetry Systems [ATS], MN) and archival temperature loggers (iButton Thermochron© Temperature Data Loggers DS1921Z-F5; Maxim Integrated, San Jose, CA). Sterile hypodermic needles and steel wire were used to secure the tag through the dorsal musculature at the base of the dorsal fin (described in Lennox, Cooke, et al., 2016). Opposite the radio tag, an iButton archival temperature logger (set to record temperature at 90 min intervals) was attached instead of the usual plastic backplate (Figure 2; see Supporting Information for calibration information). All handling and tagging were conducted in accordance with the Carleton University Animal Care and Use Committee.

FIGURE 2 Double-tagging Atlantic salmon (*Salmo salar*) with coded radio-transmitting tags (bottom) and archival temperature loggers (top). Salmon were maintained submerged in water in a PVC tube during tagging and externally tagged prior to release. Colour image available online only [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Data analysis

A 500 NOK reward for returning tags was offered to anglers that captured tagged salmon. Archival temperature loggers were recovered from 10 of the 21 salmon that were tagged (Table 1). Five were recovered from salmon that were removed from the river by harpoon on September 25, and the other five loggers were removed from salmon that were recaptured and harvested by anglers (one was recaptured as a kelt the following summer, June 20, 2015). As a result, the sampling intervals differed among individuals, with some temperature records spanning several days whereas others covered much longer periods. Our modelling was implemented to determine the relationship between fish habitat and river temperatures using linear regression in R (R Core Team, 2017). In consideration of possible differences among fish attributable to differences in fish size, fish position in the river or other factors, we generated a mixed effects linear model (*lme* function in R package nlme; Pinheiro, Bates, Debroy, & Sarkar, 2014) with fish ID as a random intercept. To determine whether the mixed effects model fit better than the fixed effects model, the mixed effects model was compared to a generalised least squares regression (*gls* function in R package nlme) with restricted maximum likelihood estimation using Akaike information criterion (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Examination of the autocorrelation function revealed residual autocorrelation, so we generated models accounting for residual autocorrelation by fish ID while accounting for time (i.e. form = ~time|fishID). Comparison of AIC values among *gls* models with different autocorrelation structures (corGaus, corExp, corLin, corSpher, corAR1, corRatio) revealed a best fit of the exponential correlation structure. Model predictions were extracted with the *predict* function and compared to actual values measured by the tags placed on the fish using linear regression.

2.4 | Bioenergetics modelling

To determine the rates of oxygen uptake of fish swum at different speeds and temperatures, hatchery-raised adult Atlantic salmon (body mass: 2.6 ± 0.4 kg; fork length: 60.6 ± 3.9 cm *SE*) were held in outdoor 4,000 L circular fibreglass tanks in ambient seawater conditions (7–11°C, dissolved oxygen >90% saturation) and seasonal photoperiod at the Centre for Aquaculture and Environmental Research (West Vancouver, BC, Canada). Food was withheld for 24 hr before experiments. A subset of fish (*N* = 22) was instrumented to measure cardiovascular parameters (data not shown here), whereas other fish were not instrumented (*N* = 14). Surgical protocols followed those detailed in Eliason, Clark, Hinch, and Farrell (2013a). The fish were anesthetised in buffered tricaine methane-sulphonate (0.1 g L^{-1} MS-222 and 0.1 g L^{-1} $NaHCO_3$; Sigma-Aldrich, Oakville, ON, Canada), weighed and transferred to a surgical table where they were maintained under a lower dose of buffered anaesthetic (0.075 g L^{-1} MS-222 and 0.05 g L^{-1} $NaHCO_3$). A 3-mm SB flow probe (Transonic Systems, Ithaca, NY) was placed around the ventral aorta, a PE-50 cannula was inserted into the dorsal aorta, and a PE-50 cannula or an oxygen probe (custom-designed; Ocean Optics, Dunedin, FL) was placed in the sinus venosus (Eliason et al., 2013a). The flow probe and cannulae/oxygen probe leads were sutured along the dorsal ridge of the fish's body using 2-0 silk sutures. Fish were placed in a Brett-type swim tunnel (220 or 400 L; described in Steinhausen, Sandblom, Eliason, Verhille, & Farrell, 2008) and allowed to recover overnight at ambient water temperatures at low water velocity (0.3–0.4 body lengths per second [bl s^{-1}]). This water velocity was sufficient to orient the fish but did not induce swimming. Similar surgeries did not impair swimming metabolism of Pacific salmon compared to controls (Eliason, Clark, Hinch, & Farrell, 2013b). The next day, resting oxygen uptake (MO_2) was measured at the ambient water temperature (ranged from 7 to 12°C over the study) and then the fish underwent a standard ramp U_{crit} critical swimming challenge (Eliason et al., 2013a). Water velocity was increased every 5 min until ~50% of the critical swimming speed (U_{crit}; ~1 bl s^{-1}) was attained. Thereafter, the water velocity was increased in smaller velocity increments (~0.15 bl s^{-1}) every 20 min until fatigue was induced (defined as the fish resting at the back of the swim tunnel for >30 s). MO_2 was measured during the second half of each 20 min interval. When the fish became fatigued, the water velocity was immediately reduced back to the resting velocity (~0.3 bl s^{-1}) and the fish was allowed to recover overnight. The next day, the water temperature was acutely increased by 2°C/hr to the warm test temperature (10–22°C). Resting MO_2 was assessed and then the fish underwent the same U_{crit} protocol described above.

To account for the allometric scaling of standard metabolic rate (Brett & Glass, 1973), we standardised the resting oxygen uptake for three fish sizes in the river, small (total length = 63.5 cm, mass = 3.03 kg), medium (total length = 89.0 cm, mass = 8.34 kg) and large (total length = 119.0 cm, mass = 20.18 kg); these lengths approximately spanned the minimum, average and maximum lengths encountered in Lakselva. Corresponding weights were derived from an empirical table of length-to-weight conversions for fish from the study site (www.lakselva.no; the table is based on fork lengths which required that we convert our total lengths to fork length by dividing by 1.046). The measured resting values of MO_2 were scaled using an equation from Steffensen, Bushnell, and Schurmann (1994), in which the $MO_2^{corrected} = MO_2^{initial} \times (Mass^{initial}/Mass^{corrected})^{(1-exp)}$, where the $MO_2^{initial}$ is the oxygen uptake of fish of $Mass^{initial}$, corrected by dividing that fish's mass by the mass of the fish of the desired size (cm; in this case, we used the three values above) and the exp is the scaling exponent 0.80 (Clarke & Johnston, 1999; Rosewarne, Wilson, & Svendsen, 2016; Steffensen et al., 1994; Winberg, 1956). The oxygen uptake data at temperatures between 7 and 22°C (above) were fit with an exponential curve for resting data and a second order polynomial relationship for fish swimming at 1.0 bl s^{-1}. Although oxygen uptake was not measured at an intermediate swim speed, we estimated oxygen uptake at 0.5 and 0.7 bl s^{-1} by interpolating from the resting and 1.0 bl s^{-1} data and fit exponential curves through the data to evaluate the internal sensitivity of our oxygen consumption equations. For these curves, values were derived using only fish at temperatures measured for both resting and swimming velocities.

TABLE 1 Summary of fish from which iButton archival temperature loggers were recovered. The table details the size of the salmon as well as the number of days the tags recorded data

Fish ID	Tagging date	Sampling interval (days)	Total length (cm)
142.144-8	July 13	73	73
142.123-14	July 14	18	97
142.213-14	July 15	4	98
142.203-12	July 16	12	91
142.123-9	July 16	70	90
142.144-11	July 17	11	80
142.213-9	July 19	67	95
142.114-8	July 30	30	111
142.123-75	August 12	126	94
142.144-112	August 28	27	66

We estimated daily oxygen uptake for fish in the river between July 13 and December 16 based on the average daily temperatures fish would have experienced given river temperatures. The HOBO river temperature logger was active in the river between July 19 and August 19; beyond these dates, the water temperatures were estimated from the iButton archival temperature loggers by back calculation using the regression equation (see Results). By fitting the regression equations to the water temperature data, daily oxygen uptake (mg O_2 kg^{-1} min^{-1}) was estimated for each day in the study period for three size classes of fish and at the four swimming speeds. Daily energy consumption was then derived by multiplying by 1,440 (minutes in a day) and by the total mass of the fish converted from the three lengths that we selected (2.67, 7.00, 17.69 kg) to calculate the mg O_2 day^{-1} consumed per fish of the three sizes. Values in mg O_2 kg^{-1} min^{-1} were multiplied by 60 to get mg O_2 kg^{-1} hr^{-1} and then multiplied by 0.00325 to convert to kcal kg^{-1} hr^{-1} based on the caloric conversion for Pacific salmon (Brett, 1995). Daily kilocalories for fish in each size class were then calculated by multiplying by the weight (kg) and by 24 (hr). Energetic scope of migrants was estimated based on equations in Jonsson et al. (1997). Energy available for migration is a function of individual length (L_{TOTAL}); the initial energy in kilojoules is described by the equation: $E = \exp(0.044 \times L_{TOTAL} + 6.99)$ and the postspawn energy described by the equation: $E = \exp(0.035 \times L_{TOTAL} + 6.51)$ and then converted from kJ to kcal by multiplying by 0.239. Projected energy depletion was calculated based on the initial energy available with a lower limit (i.e. threshold for life) considered to be the postspawn energy. Models of global temperature increase are available to project the rate of warming, but vary based on latitude and have uncertainty associated with the emissions scenario, along with concomitant changes in radiative forcing, precipitation, cloud cover, albedo, ecosystem structure, etc. (Joos et al., 2001). Instead of using specific projections, we calculated the expected energetic use for the study period at the present water temperature and for warming scenarios of 1, 2 and 4°C.

3 | RESULTS

Of the 21 salmon that were tagged, one salmon left the river prior to the spawning season and one salmon died immediately after release (see Lennox, Cooke, et al., 2016). Of the remaining 19 tagged salmon, archival temperature loggers were recovered from 10 salmon (Table 1). These salmon were mostly tagged in the lower reaches of the river and none of them transited the lakes to access upper reaches of the river or the tributary Vuolajohka (Figure 1). Therefore, no tagged salmon was recorded by the fixed receiver stations and given that all tagged fish remained in this river section ($N = 39$; Lennox, Cooke, et al., 2016), only temperature readings from the lower section of the river were used for modelling purposes (Figure 1).

We recorded a seasonal decline as well as daily oscillations in water temperature (range in daily variation = 0.48–4.21°C). Between July 16 and August 19, salmon were recorded at temperatures between 11.5 and 18.0°C (average: 14.5 ± 1.2°C). By comparison, average daily water temperatures during the same period ranged between 11.5 and 18.5°C (average: 14.8 ± 1.4°C). One salmon, which was caught by an angler in the river in the spring after its release (fish ID 142.123-75; Table 1), provided a continuous 126-day temperature log through to December 16, 2014 (Figure 3). This fish had experienced temperatures as low as −0.1°C in winter.

Comparison of the mixed effects and fixed effects models suggested a better fit of the mixed effects model rather than the generalised least squares model (ΔAIC = 708). There was a significant relationship between river temperature and fish habitat temperature ($t = 260.82$, $p < 0.01$; Figure 4). Model-predicted values of fish habitat temperature had a strong (model adjusted $R^2 = 0.94$) positive relationship to actual values. Predictions of fish habitat temperature could therefore be accurately generated using river surface temperature data by a regression equation: $t_{FISH} = 3.24 + 0.76(t_{RIVER})$.

Swim tunnel respirometry of hatchery Atlantic salmon was used to derive oxygen uptake equations as a function of water temperature (Table 2; Figure 5). Based on published equations for estimating energy content of Atlantic salmon, initial energy content of the wild salmon in Lakselva was estimated based on their length to be 48,762, 13,026 and 4,242 kcal for salmon measuring 119.0, 89.0 and 63.5 cm, respectively, with an expected depletion of 52%, 39% and 21% of somatic energy at present temperatures (Figure 6). During the 150-day modelled period (July 16 to December 16), large fish (119.0 cm) were projected to deplete the most gross energy, between 10,212 (at rest) and 47,610 kcal (swimming at 1.0 bl s^{-1}; Figure 7). Small salmon had the most extreme relative energy depletion; at rest, we estimated 52% energy depletion for small salmon but only 21% for large salmon at present temperatures (Figure 8). Projected increases in temperature to 4°C increased gross energy consumption to 65% and 26% for small and large salmon, respectively. Faster swimming speeds depleted energy more rapidly than slower speeds, demanding 169% of the somatic energy of small salmon compared to 98% from large salmon at 1.0 bl s^{-1} (present

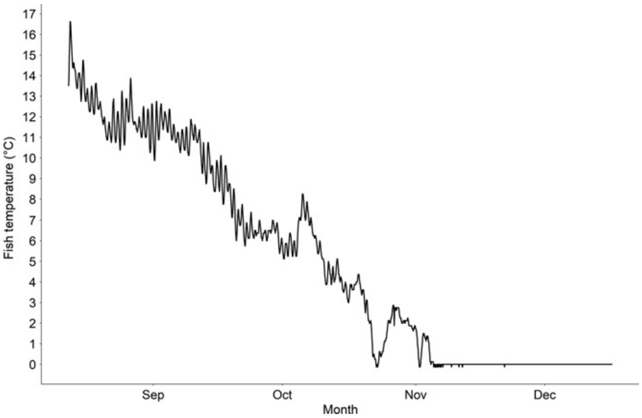

FIGURE 3 Fish thermal experience logged in Lakselva by salmon 142.123-75, whose logger remained active until December 16, 2014 (note that the values have been adjusted based on the regression analysis; see Supporting Information)

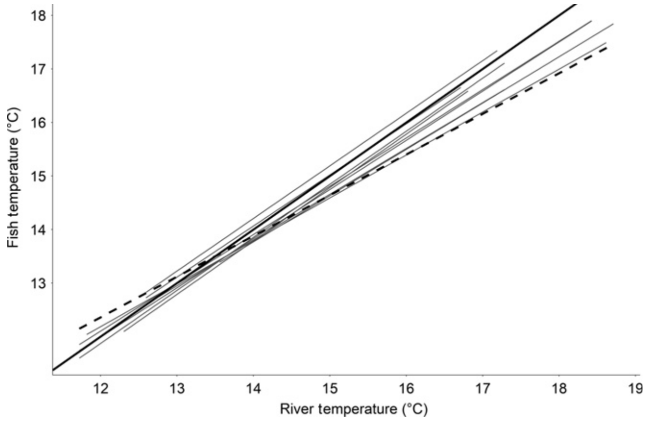

FIGURE 4 The relationship between fish temperature and the river temperature in Lakselva. Each grey line represents values from a temperature logger of an individual salmon in the river. The solid black line is the line of identity at $y = x$. Linear mixed effects modelling with an exponential temporal autocorrelation structure (see Methods) supported a linear relationship between river temperature and habitat temperature of salmon during this period and the line of prediction is illustrated by the broken black line

temperature regime). Warmer temperature (+4°C) increased caloric consumption for fish swimming at 1.0 bl s^{-1} by 9% for small individuals and 5% for large individuals (Figure 7), with less drastic effects at slower swimming speeds. Overall, this modelling revealed that an individual's activity accelerates energy depletion more drastically than warming does, and the ability to moderate swimming can effectively conserve energy across climate scenarios. Our estimates also suggest that large fish will be more resilient to temperature increases than small fish provided they can hold using a slow swimming speed during the migration.

4 | DISCUSSION

We derived a linear relationship between water temperature and fish habitat temperature for an anadromous ectotherm during its spawning migration in fresh water. The ability to predict the experienced temperature allowed us to estimate energetic expenditure. In doing so, we also provided the first equations approximating the relationship between water temperature and oxygen uptake of Atlantic salmon at various swimming speeds, and the first estimates of the energy metabolism of Atlantic salmon modelled to wild fish. Climate change is an ongoing threat to all freshwater ecosystems including in the Arctic. Understanding how key parameters, temperature, locomotion and body size, contribute to energy depletion is relevant across species, particularly as changes to the global climate will require physiological and behavioural adaptations to cope. Our finding that activity is the most substantial contributor to energy depletion suggests that animals will need to adapt their migration activity and behaviours to adjust to the increased metabolic demands associated with warmer river temperatures.

TABLE 2 Oxygen consumption equations derived from hatchery Atlantic salmon (*Salmo salar*) at rest and swimming at 1.0 bl s^{-1}. Data for 0.5 and 0.7 bl s^{-1} were interpolated. T_w is the ambient water temperature. Oxygen consumption is returned in mg O_2 kg^{-1} min^{-1} and converted to mg O_2 day^{-1} by multiplying by body size and 1,440 (min/day)

Swimming speed	Fish size	Oxygen consumption equation
Resting	Small (63.5 cm)	$MO_2 = 0.55 \times \exp(0.07 \times T_w)$
Resting	Medium (89.0 cm)	$MO_2 = 0.45 \times \exp(0.07 \times T_w)$
Resting	Large (119.0 cm)	$MO_2 = 0.38 \times \exp(0.07 \times T_w)$
0.5 bl s^{-1}	All	$MO_2 = 1.32 \times \exp(0.03 \times T_w)$
0.7 bl s^{-1}	All	$MO_2 = 1.85 \times \exp(0.03 \times T_w)$
1.0 bl s^{-1}	All	$MO_2 = 2.90 + (0.02 \times T_w) + (0.0021 \times T_w^2)$

Compared to values published for pink (*Oncorhynchus gorbuscha* Salmonidae) and sockeye (*Oncorhynchus nerka* Salmonidae) salmon, Atlantic salmon appear to have slower metabolism (Eliason et al., 2011; MacNutt et al., 2006). Regression validated that ambient water temperatures could predict fish habitat temperature in this river within the range of 11.5–18.5°C, which is within the reported range of optimal temperatures of this species (Anttila et al., 2014; Booth, 1998; Frechette et al., 2018; Mills, 1989). While ongoing increases in summer temperature may portend an increasingly energetically demanding freshwater migration, we found that the varying effects of body size and swimming speeds will play a crucial role in energy management for the response of anadromous fish to warming. Migrants that have stopped feeding necessarily economise energy during the migration to ration their energy reserves for spawning (Bernatchez & Dodson, 1987). This strategy is true for today's thermal regime and also in future years when rivers are projected to be warmer. Fleming (1998) provided a range of 52%–65% energy depletion for Atlantic salmon during the spawning migration, similar to that of migratory Arctic charr (*Salvelinus alpinus*) in Canada (52%; Dutil, 1986). However, Jonsson et al. (1997) suggested a more extreme energy depletion of 72% for salmon in the Norwegian River Drammen, similar to that of anadromous American shad (70–80%; Glebe & Leggett, 1981) but less than long-distance migrating Pacific salmon (males: 82%, females: 92%; Bowerman, Pinson-Dumm, Peery, & Caudill, 2017). The disparity within Atlantic salmon is likely related in part to body size; applying our regression equation to the ambient temperatures in the river provided a minimal (i.e. at rest) 20% depletion of somatic energy for large salmon (119.0 cm length) and 51% for small salmon (63.5 cm length).

Our estimates of energy depletion do not account for a heterogeneity in swim speeds that would include increased activity during active migration. Bowerman et al. (2017) suggested that such gait transitions would contribute to the majority of the energy depletion for migrating Pacific salmon. However, Pacific salmon have a much more extensive spawning migration distance (920 km) compared to the much shorter distance travelled by Lakselva salmon. In a corresponding manner, a large proportion of the time in fresh water is spent holding because most Atlantic salmon enter rivers weeks or

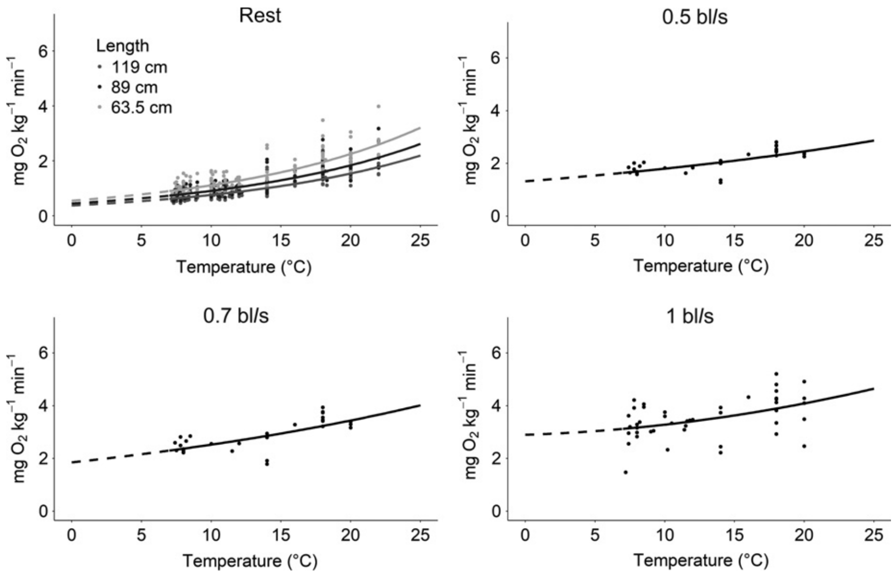

FIGURE 5 Atlantic salmon oxygen metabolism between 7 and 22°C at four swimming speeds. Values for the resting fish were mass-corrected for three sizes using a scaling exponent of 0.80 (see Clarke & Johnston, 1999). Curves are presented for three body lengths, near the minimum, mean and maximum values we encountered in Lakselva. Values for resting and 1.0 bl s^{-1} were derived from swim tunnel respirometry (see Table 2). Values for 0.5 and 0.7 bl s^{-1} were interpolated from these data by averaging the oxygen uptake values. Regression curves were fit to the plots using a polynomial (second order) equation fit to the 1.0 bl s^{-1} data and exponential curves fit at other swimming speeds. Dashed portions of the curves are extrapolations made by the regression equations beyond the temperature ranges at which oxygen uptake was measured (i.e. 0–7°C)

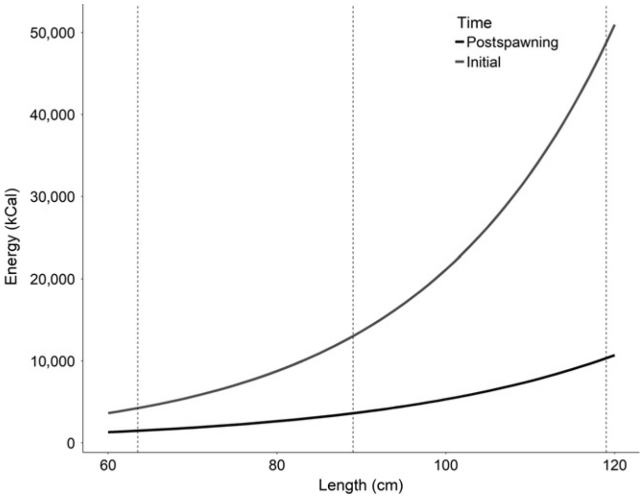

FIGURE 6 Predicted somatic energy at length (cm) of Atlantic salmon (*Salmo salar*) based on equations derived by Jonsson et al. (1997) in the River Drammen, Norway. Both curves follow exponential equations and represent measurements made in July (E_{initial} = exp [0.044 × L_{TOTAL} + 6.99]) and November, following spawning ($E_{\text{postspawn}}$ = exp [0.035 × L_{TOTAL} + 6.51]). Broken vertical lines represent the lengths we selected for our bioenergetics modelling in this study, showing the energetic scope during the freshwater migration

months in advance of spawning (Økland et al., 2001). The precise costs of swimming activity are presently not known because there are no long-term studies of migrating Atlantic salmon energetics; therefore, we generated our model at several speeds. Speed is known to be closely linked to the life history of fishes (Eliason & Farrell, 2016; Glebe & Leggett, 1981). Bernatchez and Dodson (1987) calculated the average swimming speed of Atlantic salmon (rivermouth to spawning grounds) to be 0.1 bl s^{-1} (using data from Belding, 1934), which is consistent with observations from telemetry that Atlantic salmon hold for long periods in slow-moving pools prior to spawning (Lennox, Cooke, et al., 2016; Økland et al., 2001; Richard et al., 2014). Although fish activity has been suggested to benefit energetically from burst-and-coast over steady-state swimming (Hinch & Rand, 2000; Weihs, 1974), limitations in data availability require simulations such as ours that assume continuous swimming (see McElroy, DeLonay, & Jacobson, 2012). Our model revealed that energy depletion was sensitive to changes to the rate of continuous swimming; individuals at slow swimming speeds will conserve energy across water temperature scenarios. Higher resolution data of swimming behaviour during the migration and throughout the migration (i.e. over the winter) will contribute to more complete models of the energy budget by identifying actual movement rates during all phases of a spawning migration including movement within pools.

Individual size was shown to be important to depletion of energy stores, with larger individuals depleting less energy and hence being more resilient than small to temperature increases and activity demands. We found that large size conferred considerably greater scope for activity, likely because of their higher energy reserves, whereas smaller individuals migrate with less stored energy and are likely to have greater sensitivity to temperature increases that accelerate energy depletion. Based on this, large salmon may be more

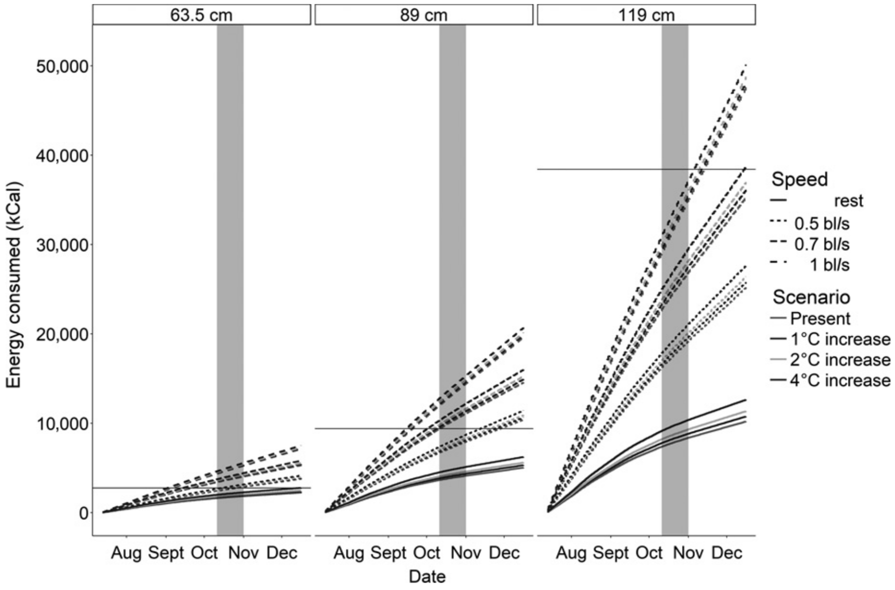

FIGURE 7 Predicted cumulative energetic expenditure (kCal) of Atlantic salmon measuring either 63.5, 89.0 or 119.0 cm, either resting or swimming at 0.5, 0.7 and 1.0 bl s^{-1} from July 13 to December 16. Monthly ticks are the first day of the noted month. Daily temperatures experienced were converted from measured river values with the regression equation: $t_{FISH} = 3.24 + (0.76 \times t_{RIVER})$ at present river temperatures or given increases of 1, 2 or 4°C. The horizontal line indicates the scope for depletion (i.e. initial energy minus postspawn energy) for each size class based on regression equations in Jonsson et al. (1997). The shaded area signifies the approximate spawning period in Lakselva, October 10–31. Energy depletion increased at higher temperatures, faster rates of movement and larger body size

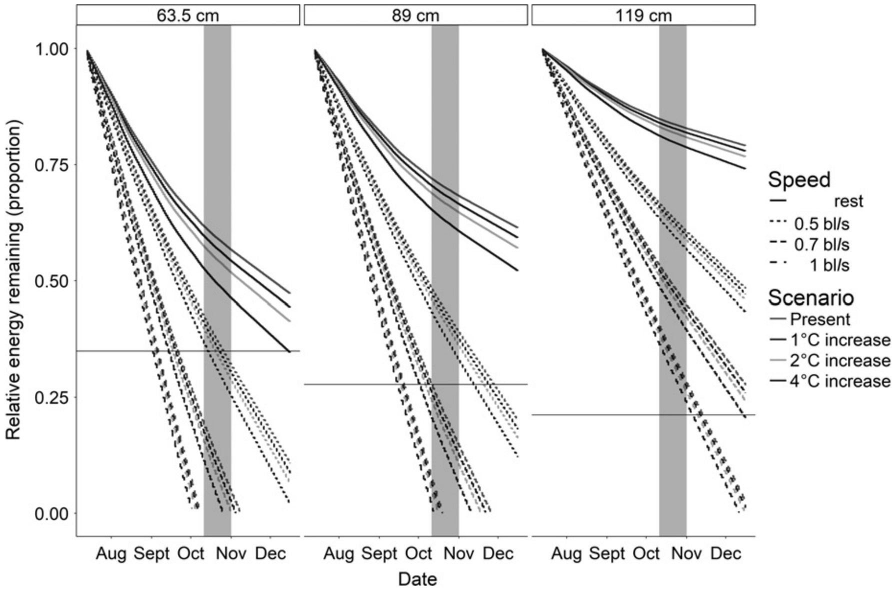

FIGURE 8 Predicted proportion of energy remaining to Atlantic salmon measuring either 63.5, 89.0 or 119.0 cm, either resting or swimming at 0.5, 0.7 and 1.0 bl s^{-1} from July 13 to December 16. Monthly ticks are the first day of the noted month. Fish habitat temperatures were calculated from the regression equation: $t_{FISH} = 1.62 + 0.88(t_{RIVER})$ at present river temperatures or given increases of 1, 2 or 4°C. The horizontal line represents the expected proportion of energy remaining in a postspawn salmon of each size based on a regression equation in Jonsson et al. (1997). The shaded area signifies the approximate spawning period in Lakselva, October 10–31. Relative energetic depletion increased at higher temperatures and for faster rates of movement but decreased with body size

resilient to climate warming and have higher fitness; however, we did not account for larger fish having a cooler optimum temperature (Morita, Fukuwaka, Tanimata, & Yamamura, 2010). Body size in Atlantic salmon is genetically and phenotypically linked to environmental factors such as the difficulty of migration and the flow regime of the natal river (Jonsson, Hansen, et al., 1991). Larger salmon also have higher fecundity and fitness (de Gaudemar, Bonzom, & Beall, 2000; Fleming, 1996). Warming of environmental temperature towards a species' optimum temperature accelerates growth and maturation, generally resulting in smaller body size at the time of maturation (i.e. the temperature-size rule; Jonsson, Jonsson, & Finstad, 2013; Kingsolver & Huey, 2008), which has been shown experimentally for semelparous salmon (Clark et al., 2012) and reef fishes (Messmer et al., 2017). The temperature-size rule has received attention in the context of climate change (e.g. Cheung et al., 2013; Daufresne, Lengfellner, & Sommer, 2009; Sheridan & Bickford, 2011), although the validity of the underlying physiological mechanisms requires further validation (Lefevre, McKenzie, & Nilsson, 2017). Our data suggest that migratory fish such as salmon could compensate for climate change with a larger size, but there are competing selective pressures. Warm ocean temperatures favour earlier maturation and smaller body size of salmon (Jonsson & Jonsson, 2004). Indeed, Atlantic salmon from warmer rivers at southern latitudes tend to mature at smaller body size (Jonsson & Jonsson, 2004, 2009).

As a relatively cold river, warming of the Lakselva River will increase the cost of freshwater residence by Atlantic salmon, with possible effects on life history such as reducing prespawn and postspawn survival (such impacts have been observed in other species, e.g. American shad *Alosa sapidissima* Clupeidae; Glebe & Leggett, 1981; Castro-Santos & Letcher, 2010). River temperatures and discharge are key factors moulding the life history of Atlantic salmon populations including smolt ages, run timing, body sizes and iteroparity (Jonsson, Hansen, et al., 1991; Power, 1981). Rivers with less annual water discharge are generally characterised by spawning runs of younger and smaller salmon (Jonsson, Hansen, et al., 1991). Sea trout (*Salmo trutta*) populations at high latitudes have less frequent iteroparity than do southern populations (Jonsson & L'Abée-Lund, 1993), a trend that may also be true of the congeneric Atlantic salmon. Phenological changes such as shifts to later run timing could also buffer energetic costs of warming water, as has been observed for populations in Newfoundland and Labrador, Canada (Dempson et al., 2017). Entering rivers later may decrease the accumulated thermal units during migration and offset energetic costs of higher water temperatures (Katinic et al., 2015) and entering earlier and swimming upriver to holding sites before temperatures become elevated will avoid a collapse in aerobic scope (Farrell et al., 2008). Late entry is generally expressed by smaller Atlantic salmon with less somatic energy than larger individuals, and perhaps the relationship can be explained by energy demands of migration (Niemelä et al., 2006; Shearer, 1990). According to Power (1981), increased water temperature promoted the evolution of a bimodal run timing distribution in Atlantic salmon to avoid movement in midsummer at high temperature (i.e. an early run and a late run establish within the same river).

Physiological acclimation to warming thermal regimes is possible when fish rear in those conditions. Anttila et al. (2014) identified significant thermal plasticity of Atlantic salmon originating from the nearby Alta River (69°58′06.3″N 23°22′29.5″E) reared in warmer water, suggesting that fish from these northern populations could adjust, to some extent, to warming conditions in fresh water depending on early life experience. In the absence of species adaptation, our estimates of energy depletion suggest that prespawn mortality of Atlantic salmon is liable to increase in a warming world. For survivors of a first reproduction, it will probably result in decreased survival and reduced iteroparity (Halttunen et al., 2013; Jonsson, Jonsson, et al., 1991). The relationship among temperature, size, activity and energy use is evidently complex and requires further investigation.

4.1 | Limitations

Although bioenergetics modelling is well established as a field of ecological inquiry, field metabolic data for fish including adult Atlantic salmon are scarce (Cooke, Thorstad, & Hinch, 2004). We used hatchery Atlantic salmon for our bioenergetic equations, an approach that may be somewhat limited; hatchery and wild salmon (and likely wild salmon of different origin) may have somewhat different conversion of energy to locomotion and future research may address this. Nonetheless, the use of surrogates is relatively common to physiological studies and surrogates of the same species should provide the most reliable information (Cooke et al., 2017). Jonsson et al. (1997) modelled somatic energy density of Atlantic salmon in the Drammen River (Jonsson et al., 1997), which are generally smaller than those in Lakselva. Thus, our energy calculation for the largest sized salmon lies beyond the data range derived for that population. Drammen is also warmer and so the salmon there spawn several weeks later than salmon in Lakselva (Heggberget, 1988). The estimates would be improved using oxygen uptake rates from wild Atlantic salmon that have entered fresh water at temperatures ranging lower than ours (min = 7°C) instead of relying on extrapolations from hatchery fish oxygen uptake. Finer scale data on the cost of swimming and the logged data on swimming effort would also improve the models (Hendry & Beall, 2004; Johnstone, Lucas, Boylan, & Carter, 1992; Lucas, Johnstone, & Priede, 1993), but would still contain inaccuracies because it is logistically difficult to perfectly estimate field metabolic rates based on swim tunnel values. Such work would have to include the oxygen debt due to anaerobic exercise (e.g. Lee, Devlin, & Farrell, 2003; Lee, Farrell, et al., 2003), especially because burst-and-coast swimming behaviours are likely to defer the immediate oxygen cost of swimming.

Like Jonsson et al. (1997), we cannot predict the energy loss through the winter months. Owing to the cold temperatures, the energy demands during this period are predicted to be small (17.53 kcal/day at 0°C at rest) compared to during the summer (48.73 kcal/day at 14.5°C at rest), as calculated for an average sized salmon (89.0 cm) for this site. Nevertheless, salmon kelts clearly have exceedingly lower energetic reserves prior to outmigration (Moore, 1997), warranting the term “spent.” Therefore, warmer winter river temperatures will accelerate energy depletion and could perhaps trigger an earlier outmigration, possibly resulting in a mismatch of outmigration and peak ocean productivity that is believed to facilitate reconditioning of spent Atlantic salmon, as it does for out-migrating smolts (Otero et al., 2014).

Intersexual differences were set aside from our analysis, yet Jonsson, Jonsson, et al. (1991) found somatic energy loss to be much greater for males than females (this is different from Pacific salmon; Bowerman et al., 2017). In a corresponding manner, more females survive spawning whereas males are more prone to die (Hawkins & Smith, 1986; Jonsson, Jonsson, et al., 1991). The minimum energy density at which salmon are capable of living and still spawning (i.e. threshold for life) has been calculated for semelparous sockeye and pink salmons and ranged between 693 kcal/kg (Hendry & Berg, 1999) and 956 kcal/kg (Crossin, Hinch, Farrell, Whelly, & Healey, 2003; Crossin et al., 2004). Bowerman et al. (2017) calculated an energy density of 860 (female) and 980 (male) kcal/kg in postspawned chinook salmon. Jonsson et al. (1997) provided an equation for estimating the somatic energy of a postspawn salmon based on length (see Methods), although their work did not identify an explicit threshold for life.

5 | CONCLUSION

As expected, energy depletion was accelerated at higher temperatures and given scenarios of higher activity. However, activity had a more profound impact on the rate of energy depletion than did increases in temperature within the modelled range. This disparity was more evident among smaller salmon than for larger individuals given that larger individuals possess greater energetic storage. Body size of Atlantic salmon is closely linked to reproductive success (de Gaudemar et al., 2000; Fleming, 1996) and salmon exhibit considerable variation in life history phenotypes across body sizes (Niemelä et al., 2006; Shearer, 1990). Our models should inspire research into how physiological plasticity and behavioural adaptations, especially run timing, could compensate for warming and should also be met with further research into interacting effects of temperature and disease (Rand et al., 2006). Ultimately, a better understanding of the behavioural and physiological mechanisms that facilitate successful migration, associated life history events (i.e. run timing, spawning) and physiological processes (i.e. cardiophysiology, biochemistry and biomechanics; Anttila et al., 2014) is necessary to understand and manage fish in a warming Arctic and advance efforts to focus conservation initiatives on sensitive populations.

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